

HOST SPECIFICITY AND PHYLOGENY OF ANOPLURA<sup>1</sup>

BY

KE CHUNG KIM<sup>2</sup>*Introduction.*

The Anoplura are an insect group of obligate ectoparasites living on the eutherian mammals. They inhabit the host body surface (skin-fur environment) and exclusively feed on blood. Their entire life cycle from egg to adult is spent on the single host. The eggs are attached to the hairs (except *Pediculus humanus* Linn.) where postembryonic development is completed. After hatching from the egg, the sucking louse passes through three nymphal stages. Each instar usually has distinct morphological characters including definitive setal density. The nymphal instars differ in size or proportion of parts and in the development of sclerotization and chaetotaxy. The second and third instars are usually similar to the adult in general appearance.

The known distribution of the Anoplura on mammals suggests that they became parasitic on the specific host groups at the early stage of eutherian mammal phylogeny except the Insectivora and that they coevolved with their hosts. Having successfully colonized the specific group of mammals, the Anoplura have developed obligate associations with their hosts involving biological adaptations — biochemical, physiological, ecological and morphological adaptations. The host associations and specificity of the Anoplura are the result of their colonization and coevolution with the host taxa.

About 500 species of the Anoplura have been recorded from approximately 32 % of the 2,600 suspected host species in the world. They are grouped into 42 genera and 15 families. The extant diversity of the sucking lice is estimated to be more than 1,000 species when all the suspected mammals are examined (Kim and Ludwig 1978).

The sucking lice are distributed throughout the world. The Anoplura fauna is especially rich in the Ethiopian region with approximately 35 % of all known Anoplura (Ludwig 1968). They are found on all major groups of eutherian mammals except the Cetacea, Chiroptera, Edentata, Pholidota, Prohoscida and Sirenia. They are absent from the Monotremata, Marsupialia and most of the land Carnivora (Fissipedia). The Insectivora are poorly colonized by the Anoplura.

Hopkins (1949) comprehensively documented the host associations of the sucking lice on mammals. This monumental work provided the basis for subsequent analyses of host associations and specificity of the Anoplura. He established a focal point on the Anoplura-mammal associations with many interpretations and theoretical alternatives for the Anoplura distribution on mammals. On the basis of the 1949 data, Hopkins (1957) further elaborated his views and theories. Since the last symposium, no attempt has been made to update the Hopkins' data-base.

This paper is based on the taxonomic and host data collected for a monograph of the Anoplura through 1978. Obvious stragglers and contamination as well as misidentifications were not included in the analysis. The higher classification of the Anoplura developed by Kim and Ludwig (1978) has been accepted here. Taxonomic status of the three nominal genera, *Galeophthirus*, *Cuyana* and

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*Lagidiophthirus*, all related to *Eulinognathus*, has not been defined. The mammal classification of Anderson and Jones (1967) is accepted and followed in this paper.

This paper presents a summary of the distribution and host associations of the Anoplura on mammals. Phylogenetic and coevolutionary relationships among the Anoplura taxa with their mammalian hosts are discussed, and theoretical alternatives are offered for the host specificity of the Anoplura.

*Distribution and Host Specificity of the Anoplura on Mammals.*

The particular suprageneric taxa usually occur on their respective specific mammalian groups, and their distribution appears to be primary, except for the Neolinognathidae, and parts of Hoplopleuridae, Polyplacidae, and Linognathidae. Diversity relationship between the Anoplura and their mammalian hosts is summarized in Table 1.

TABLE 1. — Diversity relationships between Anoplura and mammals (up to 1978). Number of known genera and species of the world is for those families with louse infestation.

Anoplura		Infested Mammals					*Mammals of World (genus-species)
Family	Genus	Species	Order	Family	Genus	Species	
Echinophthiriidae	4	11	Pinnipedia	3	17	17	20-31
	1	1	Carnivora	1	1	1	25-70
Enderleinellidae	5	50	Rodentia	1	24	80	51-261
Haematopinidae	1	16	Artiodactyla	3	11	14	75-171
	** (1)	4	Perissodactyla	1	1	3	6-16
Hamophthiriidae	1	1	Dermoptera	1	1	1	1-2
Hoplopleuridae	5	134	Rod., Lag., Ins.	11	75	289	321-1709
	(Hoplopleurinae)	2	124	Rodentia	6	65	270
(Haematopinoidinae)	(1)	1	Lagomorpha	1	1	3	1-14
	1	7	Rodentia	2	6	14	11-34
	2	3	Insectivora	2	3	4	39-313
Hybophthiriidae	1	1	Tubulidentata	1	1	1	1-1
Linognathidae	3	56	Artiodactyla	3	31	59	62-152
	(1)	4	Carnivora	1	4	11	15-41
Microthoraciidae	1	7	Hyacoidea	1	3	11	3-11
	1	4	Artiodactyla	1	2	4	2-4
Neolinognathidae	1	2	Insectivora	1	1	4	5-28
Pecarocidae	1	1	Artiodactyla	1	1	1	1-2
Pedicinidae	1	14	Primates	1	6	27	11-60
Pediculidae	1	4	Primates	3	6	14	16-38
Polyplacidae	8	157	Rodentia	34	89	302	354-1687
	2(1)	7	Insectivora	3	7	19	5-15
	1	6	Lagomorpha	1	3	11	8-49
Ratemiidae	3	7	Primates	3	6	8	14-30
	1	2	Perissodactyla	1	1	4	1-7
Pthiridae	1	2	Primates	2	2	2	5-9

\* After Anderson and Jones (1967).

\*\* Number in parenthesis indicates the genus already counted for the family.

The Echinophthiriidae are exclusively parasitic on aquatic carnivores, primarily the Pinnipedia. Of five recognized genera only *Latagophthirus* remains to be endemic to the Fissipedia. *Latagophthirus* is presently monotypic; *L. rauschi* Kim and Emerson is from the river otter, *Lutra canadensis*. It is expected that *Enhydra lutris* (sea otter) harbors a species of *Latagophthirus* (Kim and

Emerson 1974). The monotypic *Echinophthirius* is widely found on the phocine Phocidae, and *Lepidophthirus* with two extant species is found on the monachine Phocidae, *Monachus monachus* and *Hydrurga leptonyx*. *Proechinophthirus* is confined to the fur seals, Arctocephalinae, of the Otariidae. *Antarctophthirus* is the most diverse taxon including six known species from a wide range of hosts throughout the Pinnipedia : Otariidae, Odobenidae, and Monachinae (Phocidae). No echinophthiriid species is synhospitalic except two species found on *Callorhinus ursinus* (northern fur seal), *Antarctophthirus callorhini* (Osborn) and *Proechinophthirus fluctus* (Ferris), which show definite microhabitat selection (Kim 1971, 1972, and 1975).

*Haematopinus* (Haematopinidae) is a generalized taxon with many primitive characters, and is widely distributed on the ungulates, Artiodactyla and Perissodactyla : primarily Suidae, Bovidae and Cervidae, and Equidae, respectively. Considering the present distribution and relatively generalized morphology, the Haematopinidae were more widely distributed on the ungulates during the Tertiary period when the ungulate diversity was greater.

*Microthoracius* constituting the monotypic family Microthoraciidae with four known species is exclusively parasitic on Camelidae in both New and Old Worlds. The monotypic *Pecarococcus* (family Pecarococidae) is a large, elongated louse parasitic on peccaries (Tayassuidae, Artiodactyla) in Southwestern United States and Central America.

*Pediculus* along with *Pedicinus* and *Pthirus* are parasites of the anthropoid Primates. *Pediculus* is found on man (Hominidae), great apes (Pongidae) and New World monkeys (Cebidae). While *P. humanus* Linnaeus and *P. schaeffi* Fehareholz are distinct, taxonomic status of other nominal species and subspecies is presently uncertain.

TABLE 2. — Host Specificity of Anoplura on Mammals.

Anoplura (families)	Total Number of Species	* Percent Specificity	Number of Louse Species with Hosts of :				
			1 specie	2 species	3 species	4 species	5 or more species
Echinophthiriidae	12	75	9	1	—	—	2
Enderleinellidae	50	66	33	9	4	1	3
Haematopinidae	20	95	19	1	—	—	—
Hamophthiriidae	1	100	1	—	—	—	—
Hoplopleuridae	134	62	83	19	17	7	8
(Hoplopleurinae)	(124)	(61)	(76)	(18)	(15)	(7)	(8)
(Haematopinoidiinae)	(10)	(70)	(7)	(1)	(2)	(—)	(—)
Hybophthiriidae	1	100	1	—	—	—	—
Linognathidae	67	66	44	15	3	4	1
Microthoraciidae	4	25	1	2	1	—	—
Neolinognathidae	2	0	—	1	1	—	—
Pecarococidae	1	100	1	—	—	—	—
Pedicinidae	13	54	7	1	4	—	1
Pediculidae	4	75	3	—	—	—	1
Polyplacidae	173	58	101	21	15	8	28
Ratemiidae	2	50	1	—	1	—	—
Pthiridae	2	100	2	—	—	—	—
ANOPLURA (Total)	486	63	306	70	46	20	44

\* % of total species that utilize a single host species.

*Pthirus* is a peculiar taxon with two known species and has been recognized to constitute a family, Pthiridae (Kim and Ludwig 1978). *P. pubis* Linnaeus is parasitic on man, while the second species *P. gorillae* Ewing is found on gorilla. *Pedicinus* (Pedicinidae) is exclusively parasitic on Old

World monkeys (Cercopithecidae, Primates). *Pedicinus* has some similarity to the forms of Hoplopleuridae and Polyplacidae.

The montypic *Hybophthirus* (family Hybophthiriidae) is a very distinct louse parasitic on the monotypic *Orycteropus afer* (aardvark) (Orycteropodidae, Tubulidentata) in Africa. *Hamophthirus* and *Neolinognathus*, each constituting a monotypic family, are highly specialized lice, parasitic on colugos or flying lemurs (*Cynocephalus*) (Cynocephalidae, Dermoptera) and elephant shrews (*Elephantulus*) (Macroscelidae, Insectivora) respectively. At present the affinities of these taxa are obscure.

*Ratemia* (family Ratemiidae) with two species is known from Equidae (Perissodactyla), of which *Equus* is the only extant genus. *Ratemia* possesses many linognathid characters.

The family Linognathidae represents a homogeneous group of Anoplura and consists of three genera, *Linognathus*, *Solenopotes* and *Prolinognathus*. *Linognathus* is primarily parasitic on Bovidae and Giraffidae (Artiodactyla) and several species are also found on Canidae (Carnivora). *Solenopotes* parasitizes Bovidae and Cervidae (Artiodactyla), while *Prolinognathus* is found exclusively on hyraxes (Procaviidae, Hyracoidea). Weisser (1975) considered the three genera monophyletic despite the remote relationships of their hosts, and suggested that protolinognathids might have colonized ancestral hyraxes secondarily through bodily contact, since the Artiodactyla used to be mostly small forms which were frequently in close contact with the Procaviidae during their evolution in Africa.

The Enderleinellidae are a homogeneous group exclusively parasitic on squirrels (Sciuridae, Rodentia), with five known genera. *Enderleinellus* is a generalized taxon widely distributed throughout the Sciuridae, and *Werneckia* is found on African squirrels, primarily *Paraxerus*. The three other genera, *Microphthirus*, *Phthirunculus* and *Atopophthirus*, are highly specialized and parasitic on flying squirrels (Petauristinae). *Microphthirus* is the parasites of the North American flying squirrel (*Glaucomys*) and *Phthirunculus* is found on the giant flying squirrels (*Petaurista*) in the Oriental region.

The Hoplopleuridae, the second largest family, is parasitic on a wide range of hosts including rodents, pikas, moles and shrews. *Hoplopleura* is widely distributed throughout the Rodentia and pikas (Ochotonidae, Lagomorpha). The diversity is concentrated on the muroid rodents such as Cricetidae and Muridae. *Pterophthirus* is parasitic on the hystericomorph Rodentia, primarily Echimyidae and Caviidae. These two genera constitute the subfamily Hoplopleurinae. The subfamily Haematopinoidea consists of *Anistroplox*, *Haematopinoidea*, both found on the Insectivora, and *Schizopthirus*, which is parasitic on dormice (Gliridae) and jumping mice (Zapodidae). *Ancistroplox* is parasitic on shrews (Soricidae), while *Haematopinoidea*, a monotypic genus is exclusively found on moles (Talpidae).

The Polyplacidae, the largest family, is a diverse group of the Anoplura parasitic on a wide range of mammals, the Rodentia, Lagomorpha, Insectivora, and prosimian Primates. The taxonomic relationships of the polyplacid genera are still confusing and very difficult to assess at present. *Polyplax* is primarily parasitic on two myomorph rodents, Cricetidae and Muridae and shrews (Soricidae). The monotypic *Proenderleinellus* is found on *Cricetomys* (Muridae) in central and western Africa. *Fahrenholzia* is primarily parasites of the Heteromyidae in western North America and Central America.

*Neohaematopinus* is primarily parasitic on the Sciuridae. Two species, *N. inornatus* (Kellogg and Ferris) and *N. neotomae* Ferris, are known from *Neotoma* (Cricetidae) in North America and *N. chlorotalpae* (Benoit) known from an insectivoran *Chlorotalpa leucorhina* (= *C. stuhlmanni*) (Chrysochloridae) in Central Africa. *Alenaphthirus* was first recognized by Benoit (1969) with *A. spinosissimus* Benoit from *Tamiscus vulcanorum* in Central Africa. Recognition of *A. spinosissimus* was based on the third nymphal instars which were being molted. The adults of *Alenaphthirus* are typically very similar to *Neohaematopinus*, while the nymphs are of hoplopleurid type with ventral tubercles on head, antennae and coxae.

*Eulinognathus* is parasitic on many different groups of rodents, *Pedetes* (Pedetidae) and Bathyergidae (mole rats) in central and southern Africa, *Hypogeomys* in Madagascar and *Lophiomys* in Africa (both in the Cricetidae), Dipodidae in northern Africa, Asia Minor, and northern Arabia eastward through southern Russia and Turkestan to Mongolia and northeastern China, *Ctenomys* (Ctenomyidae), and Chinchillidae in South America. Related to this genus, *Lagidiophthirus* and *Cuyana* are

known from *Lagidium* (Chinchillidae) in South America, and *Galeophthirus* from *Galea* (Caviidae). Taxonomic status of these genera related to *Eulinognothus* is not clarified at present.

*Ctenophthirus* and *Scipio* are aherrant taxa parasitic on the hystricomorph Rodentia. *Ctenophthirus*, a highly specialized montypic genus, is found on *Cercomys* (Echimyidae) in South America, but *Scipio* is parasitic on African hystricomorphs, *Thryonomys* (Thryonomyidae) and *Petromus* (Petro-myidae). *Haemodipsus* is endemic to the Lagomorpha (Leporidae). The known species of *Haemodipsus* are distributed in the Holarctic region and Africa.

*Sathrax* and *Docophthirus* are successful colonizers of tree shrews (Tupaïidae, Insectivora) in southeastern Asia. *Sathrax* is found on *Tupaia*, while *Docophthirus* is from *Anathano*. There are three highly specialized taxa on the prosimian Primates: *Lemurphthirus* on Lorisidae, *Lemurpediculus* on Lemuridae, and *Phthirpediculus* on Indridae. Their taxonomic relationships to typical polyplacids are not clear.

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## DISCUSSION

LAVOCAT. — Les Polyplacidae, et en particulier le genre *Polyplax* sont parasites de différents groupes de Rongeurs. Trouve-t-on le même genre en Afrique et en Amérique du Sud ?

KIM. — There are two genera, but they are closely related.

LAVOCAT. — Comment expliquez-vous cette distribution ? Elle pourrait être la preuve de relations entre les Rongeurs sud-américains et africains. Le genre présente-t-il une distribution holarctique ?

KIM. — Well, this is not really clear, we must work more on this.